

Natural Hybridization between the Clupeid Genera *Dorosoma* and *Signalosa*, with a Report on the Distribution of *S. petenensis*¹

W. L. MINCKLEY & LOUIS A. KRUMHOLZ

Department of Biology, University of Louisville, Louisville, Kentucky

(Plates I & II; Text-figures 1 & 2)

FISHES of the order Clupeiformes are virtually world-wide in distribution (Berg, 1940), and include a great variety of species. The systematics of the group, including the family Clupeidae which contains some of the more important commercial food fishes as well as many others, has been studied intensively. Despite the volume of research on classification, there are no records of natural hybridization between any clupeid species in North America (Hubbs, 1955).

This paper is concerned with the description of apparently the first known hybrids between the threadfin shad, *Signalosa petenensis* (Günther), and the gizzard shad, *Dorosoma cepedianum* (LeSueur). In addition, there is a report on recent findings regarding the range of the threadfin shad.

Here, it seems appropriate to discuss briefly the generic status of these two species, both of which have been placed in the genus *Dorosoma* by some recent workers. At present, "lumping" of genera of North American freshwater fishes sometimes occurs with alarmingly little data to substantiate the change. Sometimes, however, the synonymization is validated on the grounds of new or re-evaluated data on morphology, ecology and distribution, and on the incidence of hybridization between species assigned to different genera. The latter, for example, was utilized by Bailey, Winn & Smith (1954) in merging the percid genera *Percina* and *Hadropeternus*, an action that may have been premature according to Hubbs & Strawn (1957a:58). Al-

though the identification of hybrids between *Dorosoma* and *Signalosa* may add credence to their congeneric identity, we feel that the genera should be regarded as distinct until a thorough study is made of the group. Until such time, we believe that the characters used to distinguish these genera, as summarized by Miller (1950: 389-391) and by Moore (1957:59-60), are sound, notwithstanding the more recent assignment of *Signalosa* to subgeneric rank under *Dorosoma* by Miller (1960:373). Additional evidence that supports the validity of these two genera is being studied in this laboratory and concerns anatomical differences in the pharyngeal pouches.

Until 1945, the genus *Signalosa* was considered to include three species: *S. petenensis*, *S. atchafalaya* Evermann & Kendall and *S. mexicana* (Günther). Hubbs (in Hubbs & Allen, 1945:116) relegated the nominal species to subspecific rank under *S. petenensis*. As indicated by Miller (1950), differences exist between these forms that indicate the need for an exhaustive revision. Until the problem is resolved it seems unwise to use other than the binomial designation.

All fishes used in this study were collected as part of the Ohio River Valley Water Sanitation Commission—University of Louisville Aquatic-Life Resources Project on the Ohio River. We are grateful to these organizations for the use of this material and to the numerous personnel who took part in the investigation.

We acknowledge the assistance of Drs. Robert R. Miller and Reeve M. Bailey of the University of Michigan Museum of Zoology, for verifying our identifications of the hybrid

¹Contribution No. 33 (New Series) from the Department of Biology, University of Louisville, Louisville 8, Kentucky.

specimens and for supplying x-ray pictures of the hybrids. Also, we acknowledge the assistance of Dr. E. L. Pirkey of the University of Louisville for x-ray pictures of the *Dorosoma* and *Signalosa*. We are grateful to Charles B. Stone for taking the photographs shown in Plates I and II.

MATERIALS AND METHODS

Body measurements and meristic counts of specimens used in this study were made following the methods of Hubbs & Lagler (1958) and Miller (1950). The study specimens are catalogued in the collection of the University of Louisville, Department of Biology. Data were collected from 25 specimens of each species and from 6 hybrid specimens. Catalogue numbers and locality data for the specimens examined are as follows: *D. cepedianum*—UL 9054, Ill., Massac Co., Massac Creek, at confluence with Ohio River, Sept. 9, 1957; and UL 9655, Ky., Jefferson Co., Ohio River, Lock No. 41, at Louisville, Jan. 30, 1958. Hybrids—UL 11372, Ky., Ballard Co., Ohio River, near Mound City, Pulaski Co., Ill., Aug. 26, 1959 (1 specimen, Pl. II, B); UL 11407, Ky., Jefferson Co., Ohio River, Lock No. 41, at Louisville, Aug. 13, 1959 (4 specimens, Pl. I, B-D, Pl. II, A); and UL 11543, same locality as UL 11407, Sept. 9, 1959 (1 specimen, Pl. II, C). *S. petenensis*—UL 7529, Ky., Henderson Co., Green River, Lock No. 1, at Spottsville, July 9, 1957; UL 10982, Ky., Jefferson Co., Ohio River, Lock No. 41, at Louisville, July 6, 1959; and UL 7562, Ky., Lyon Co., Cumberland River, Lock "F," July 11, 1957. Plates I and II are photographs of specimens of *D. cepedianum* from UL 9655 (Pl. I, A), the 6 hybrids, and of *S. petenensis* from UL 10982 (Pl. II, D).

CHARACTERS OF THE HYBRIDS

As in the case of most papers dealing with natural hybrids, our evidence of hybridization between *S. petenensis* and *D. cepedianum* is circumstantial; however, this type of evidence has been validated by comparisons of natural and experimentally produced hybrids (Hubbs & Hubbs, 1932; Hubbs, 1956; Hubbs & Strawn, 1957b; Linder, 1958; and others), and strongly supported by the great numbers of natural hybrids that have been described in recent years (Hubbs, 1955). Our hybrids between *Signalosa* and *Dorosoma* show few characters that fall near true intermediacy, but exhibit a composite of the characters of each genus. The relative intermediacy of characters in hybrids may be readily shown by calculation of the hybrid index, as defined by Hubbs, Hubbs & Johnson (1942:7) using the following formula:

$$\frac{M^h - M^1}{M^2 - M^1} = \text{Hybrid Index}$$

in which the value of M^h equals the mean value for the given character in the hybrid specimens, M^1 equals the mean for the parental species assigned the value of 0 (*D. cepedianum*), and M^2 equals the mean for the parental species assigned the value of 100 (*S. petenensis*). The results of these calculations are shown in Text-fig. 1.

PROPORTIONAL MEASUREMENTS

Length of Head.—This measurement differs little between the two presumed parental species (Table I). The ranges overlap widely in the parental species, with *D. cepedianum* being much more variable than either *S. petenensis* or the hybrid specimens. The measurements of the hybrids are intermediate (Text-fig. 1, Table I), but the lower variation corresponds with the threadfin shad.

Distance from Origin of Dorsal Fin to Snout (Predorsal Length).—In this character the hybrids are intermediate, but tend toward *S. petenensis*. This tendency appears to be a result of shortening of the body between the origin of the dorsal fin and the nape in the hybrids, rather than an extreme shortening between the nape and the snout. In the latter measurement the hybrids fall midway between the parental species (Text-fig. 1), whereas in the remaining distance from the nape to the origin of the dorsal fin, the hybrids are closer to *S. petenensis*, as is shown by the following data on the means and ranges (ranges in parentheses) for the gizzard shad, hybrids and threadfin shad, respectively: nape to snout, 184 (167-198), 189 (180-194) and 194 (180-207), hybrid index 50 percent.; origin of dorsal fin to nape, 311 (274-344), 277 (233-301) and 268 (255-274), hybrid index 79 percent.

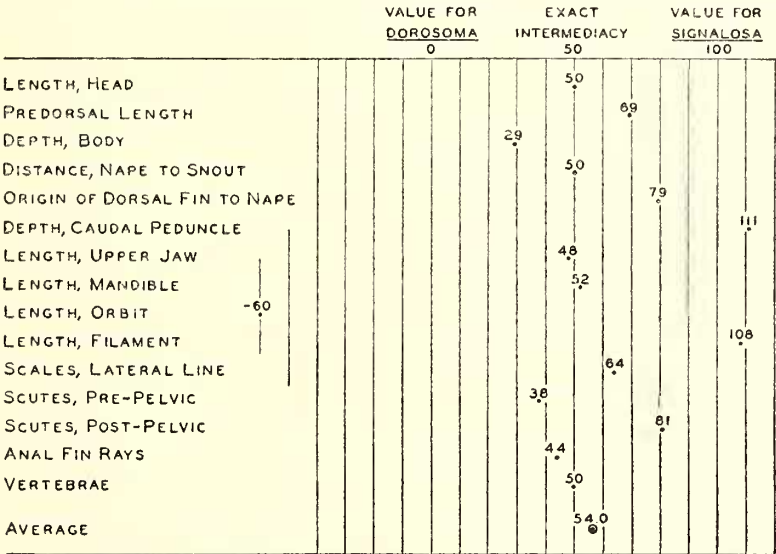
Depth of Body.—In the greatest depth of body, the hybrids resemble the gizzard shad more closely than the threadfin shad. It is of interest to point out here that measurements of body depth and caudal peduncle depth (see below) each tends toward the parental species that has the larger measurement. The tendency for the hybrid clupeids described here to range toward the parental species that exhibited the more extreme development of the character of body depth and caudal peduncle depth possibly could be ascribed to hybrid vigor ("heterosis"). Hubbs & Hubbs, (1931, 1933) found that hybrid centrarchids tended to grow faster and be relatively heavier than either of the parental stocks. Hubbs & Miller (1943:370-371) determined that depth of head, body and caudal pe-

TABLE I. STANDARD LENGTHS IN MILLIMETERS, AND PROPORTIONAL BODY MEASUREMENTS OF 25 *D. cepedianum*, 6 HYBRIDS, AND 25 *S. petenensis* FROM THE OHIO RIVER BASIN. Measurements are expressed as whole numbers calculated as thousandths of standard length. Means are followed by plus or minus one standard deviation. Ranges are in parentheses, with values for each hybrid listed separately.

Character	<i>Dorosoma</i>	Hybrids						<i>Signalosa</i>
		UL 11372		UL 11407		UL 11543		
Standard length	119.4 (91.8-148.3)	154.1	161.7	135.8	146.3 145.3	136.4	144.3	102.7 (90.5-147.0)
Length of head	284 ± 18.46 (256-313)	287	281	282	285 ± 4.44 279	290	288	286 ± 2.32 (253-303)
Predorsal length	494 ± 13.72 (462-535)	475	472	469	472 ± 2.96 475	468	473	462 ± 14.80 (422-478)
Depth of body	358 ± 14.60 (330-385)	349	341	342	347 ± 8.26 357	356	337	320 ± 16.40 (294-355)
Depth of caudal peduncle	97 ± 4.95 (88-110)	107	104	108	107 ± 2.13 109	104	107	106 ± 6.85 (90-115)
Length of upper jaw	69 ± 7.16 (55-84)	80	77	80	79 ± 3.06 75	79	84	90 ± 5.48 (76-98)
Length of mandible	91 ± 7.65 (78-106)	103	101	108	106 ± 4.56 102	106	114	120 ± 6.78 (104-130)
Length of orbit	76 ± 7.45 (61-89)	69	66	73	70 ± 2.49 70	72	71	86 ± 4.61 (75-93)
Length of dorsal filament	183 ± 36.30 (107-260)	364	343	346	350 ± 8.94 354	340	355	337 ± 24.90 (255-365)

dunele, as well as certain other eharacters, were extreme in hybrids between *Siphateles mohavensis* Snyder and *Gila orcutti* Eigenmann & Eigenmann, and attributed this to heterosis. The over-all aspect of our hybrid specimens suggests a greater "plumpness" of body than either of

the parental species. On the basis of the present specimens, the parental species have a diverging length-weight relationship with increase in length, and the hybrid specimens fall on the heavier side of *D. cepedianum*. We hesitate, however, to use the term heterosis when refer-



TEXT-FIG. 1. Average values (hybrid indices) for all statistically analyzed characters, excluding Pectoral Fin Rays for which the hybrid index was -500, for the six *Dorosoma* × *Signalosa* hybrids on a percentage scale in which the average values for *Dorosoma* are arbitrarily set at 0 and those for *Signalosa* at 100.

ring to excessive growth or extreme characters of interspecific hybrids. Rather, we prefer to follow Dobzhansky (1952:222-223) in distinguishing between true heterosis and luxuriance, heterosis representing "normal adaptive states attained in outbred sexual species as a result of an evolutionary history controlled by natural or by artificial selection," and luxuriance pertaining to "an accidental condition brought about by complementary action of genes found in the parental form[s] crossed."

Depth of Caudal Peduncle.—The mean value for the depth of the caudal peduncle of the hybrids corresponds with that of *S. petenensis* (see above).

Length of Upper Jaw and Length of Mandible.—Measurements of both of these characters approximate the general intermediacy of hybrid fishes. However, the means of both characters tend toward the mean of *D. cepedianum*.

Length of Orbit.—Orbital length in the hybrids was less in proportion to standard length than in either parental species (Table I). The small eye of the hybrids lies near the lower range of variation in *D. cepedianum*, and may be a result of the consistently larger size of the hybrids as compared with the smaller average size of both the parental species. Miller (1950) indicated that the eye (orbital length) becomes progressively smaller in proportion to body length in the three southern species of *Dorosoma* (*D. anale* Meek, *D. clavesi* Meek and *D. smithi* Hubbs & Miller). He observed that these proportional changes also appeared to occur in the specimens of *D. cepedianum* that he examined, but too few of these were available for a conclusive analysis.

Length of Dorsal Filament.—Mean length of the dorsal filament in the hybrid specimens exceeds that in either of the parental species (Textfig. 1). The mean length of the filament of *S. petenensis* greatly exceeds that of *D. cepedianum*, with scarcely any overlap (Table I). The excessive growth of the dorsal filament in the hybrids may be an expression of luxuriance, which corresponds with the condition of heterosis cited as the most probable reason for enlargement of the fins in certain hybrid cyprinids by Hubbs & Miller (1943).

Two similar theories have been advanced pertaining to the extremeness of characters found in hybrid fishes. The length of the dorsal filament and the near-extreme values for the characters discussed above may be a result of varied developmental rates in the parental species as postulated by Hubbs & Strawn (1956, 1957b) for experimentally propagated hybrids in the Cyprinidae and Percidae. In this explana-

tion, the rate of development of a character changes at certain times during ontogeny and the points at which these changes occur were called "points of inflection" by Martin (1949). Hubbs & Strawn (1957b:9) stated that if the "hybrid individual had the point of inflection of one species for the initiation of the period in which that character was laid down and the point of inflection of the other species for the stopping point, that hybrid could be more extreme than either parent." This theory is similar to that of Hubbs & Kuronuma (1942) who attributed the lack or diminution of numbers of tubercles on the blind side of hybrid flounders to an additive effect of two genetic factors, both of which tended toward reduction of the character. Such an additive effect could function in the reverse situation, thus causing a tendency for a greater expression of a character. Miller (1950: 405-407) found that the dorsal filament of *D. cepedianum*, *D. anale* and *D. smithi* increased in relative length with age, "at least up to a certain size range." Our data on gizzard shad substantiate this. This phenomenon, however, does not appear to be present in 40 specimens of threadfin shad that we examined. Thus, in line with the reasoning of Hubbs & Kuronuma (*op. cit.*), the elongation of the filament in the hybrids could have resulted from an additive effect of factors that control the proportional increase in filament length in the gizzard shad with increased size, acting in conjunction with factors that control the consistently greater length of filament in *S. petenensis*.

MERISTIC CHARACTERS

Scales in the Lateral Line.—There was a marked difference between *Signalosa* and *Dorosoma* in the number of lateral-line scales, and no overlap occurred in the counts of our specimens (Table II). The mean and range of the lateral-line scales of the hybrids falls between the maximum for *Signalosa* and the minimum for *Dorosoma*. The parental species differ markedly not only in the numbers of scales, but in the pattern of scales on the body (Miller, 1950). In the threadfin shad, the scales are arranged in regular series on the body and are loosely attached and extremely thin. In *Dorosoma*, the scale rows are irregular, the scales are thicker and are more often embedded in the epidermis, especially on the anterior part of the body. In the hybrids, both mean number of scales and general pattern of scalation tend toward *Signalosa*.

Pre- and Post-pelvic Scutes.—In the parental species, there was an overlap in the number of

TABLE II. MERISTIC COUNTS OF 25 *D. cepedianum*, 6 HYBRIDS, AND
25 *S. petenensis* FROM THE OHIO RIVER BASIN.
Means are followed by plus or minus one standard deviation. Ranges are in parentheses,
with values for each hybrid listed separately.

Character	<i>Dorosoma</i>	Hybrids						<i>Signalosa</i>
		UL 11372		UL 11407		UL 11543		
Scales in lateral line	62.5 ± 2.34 (59-67)	51	50	51.5 ± 1.95 51 55	50	52	45.4 ± 1.63 (42-48)	
Pre-pelvic scutes	18.0 ± 0.30 (17-19)	17	18	17.2 ± 0.78 16 17	17	18	15.9 ± 0.53 (14-17)	
Post-pelvic scutes	11.6 ± 0.80 (10-12)	11	11	11.0 ± 0.63 11 11	10	12	11.1 ± 0.03 (10-12)	
Rays in anal fin	30.4 ± 1.74 (25-33)	28	29	27.2 ± 1.73 27 27	28	24	23.2 ± 1.33 (20-25)	
Rays in pectoral fin ¹	14.5 ± 0.96 (12-16)	16-16	16-16	16.0 ± 0.00 16-16 16-16	16-16	16-16	14.2 ± 0.49 (14-15)	
Vertebrae	49.7 ± 0.40 (48-51)	47	46	46.3 ± 0.62 46 46	46	47	42.9 ± 0.58 (41-44)	

¹All rays, including rudiments, were counted on both right and left fins.

pre-pelvic scutes but the means were significantly different. The counts for the hybrids were intermediate (Text-fig. 1). For the post-pelvic scutes, the range was the same for each parental species as well as the hybrids, and there was no significant difference in the means (Table II).

Rays in the Anal Fin.—Ranges in the number of anal fin rays in *Dorosoma* and *Signalosa* usually do not overlap in areas of sympatry (Miller, 1950). One of the present specimens of *D. cepedianum* had 25 anal rays, equal to the highest count that we obtained for *S. petenensis*. The mean count for the hybrids was intermediate, but varied toward the mean for the gizzard shad.

Rays in the Pectoral Fin.—The number of rays in the pectoral fins of the hybrids was extremely high and very constant compared with those of the parental species. The theory of complementary points of inflection for the development of certain characters was used to explain the extreme numbers of fin rays found in hybrid fishes by Hubbs (1956) and by Hubbs & Strawn (1957b).

Vertebrae.—The mean count of 46.3 vertebrae in the hybrid specimens falls between counts obtained for the parental species (Table II, Text-fig. 1). Miller (1950), on the basis of counts from 30 *Signalosa* and many *Dorosoma*, cited 40 to 45 and 43 to 51, respectively, for the two genera, with 47 to 51 for *Dorosoma* where its range overlaps that of *Signalosa*. Our counts of vertebrae were made from x-ray photographs using the technique of Miller (*loc. cit.*).

PIGMENTATION

The following color notes were made both from preserved and freshly caught specimens. Fish were preserved in formalin, washed in water, then placed in 35 percent. isopropyl alcohol, a preservative that removes all but the basic color patterns. Notes taken from fresh specimens are placed in quotes. One hybrid specimen (Pl. II, C) died before it was preserved and because of the loss of color is not included in the descriptions. Only one of the hybrids was recognized in the field and consequently notes pertaining to yellow pigments in the hybrids refer only to that specimen, UL 11372, taken near Mound City, Illinois.

Head.—*D. cepedianum*: brownish on dorsum; dorso-lateral region with a spot postero-dorsal to eye (very diffuse); upper one-third of opercle pigmented, in some specimens pigment extending down to include upper one-half; "lower part of head silvery, sometimes with a slight suffusion of bronze" (Pl. I, A). Hybrids: brownish cap present on upper surface of head as in *Signalosa*, with indication of unpigmented spot postero-dorsal to eye (in three specimens); opercle pigmented on dorsal one-third (in one), intermediate (in two), and as in *Signalosa*; "head yellow below, becoming intense canary yellow in branchiostegal region;" snout as in *Signalosa* (in two) mustache weakly developed (in one), and absent; chin white (in three) to weakly pigmented; black inside mouth strongly (in two) to weakly present as scattered melanophores along posterior edge of mandible (Pl. I,

B-D, Pl. II, A-C). *Signalosa*: dark brownish-black over top of head, extending from nape at level with upper edge of eye, forward over eye to snout; upper edge of opercle pigmented, extending down as scattered melanophores to approximately middle eye; "lower part of head yellowish, tending toward canary yellow, in the branchiostegal region;" snout with a "mustache of melanophores distinct on the maxillary" (present also in preserved material); chin with scattered melanophores, with intensified area inside mouth on mandible (Pl. II, D).

Body.—*D. cepedianum*: dorsal region brown to brownish-black, extending one-third of distance down side; scales with thin band of melanophores near posterior edge in area of dorsal pigment; extreme dorsal area dark in a discrete band; humeral spot diffuse, brownish-black confluent with, and diffusing into, dorsal pigment on postero-dorsal and dorsal sides, sharply outlined anteriorly by light area; spot equal to orbit, to slightly larger; humeral bar present (an extension of head pigment down cleithrum beneath opercle), extending to lower edge of opercle; lateral region, breast and posterior body uniform silvery, dorsum sometimes with a bronze cast, with faint punctulations along lateral area in some specimens; fin bases with scattered melanophores. Hybrids: dorsal pigment brownish-black to brown, extending one-fourth (in two) to one-third distance down side; scales with dorso-ventrally diffuse groups of melanophores, forming distinct lines along sides; humeral spot jet black, bordered before and below by light areas, upper one-third of spot bordered by (in four), and diffusing into, dorsal pigment; humeral spot slightly smaller than eye (in four) to equal or slightly larger; humeral bar present to lower edge of opercle (in one), one-half of distance (in three), to slightly developed; "lower abdominal area as in *Signalosa* (in one); lateral region as in *Signalosa*; postero-ventral side silvery except at fin bases, where canary yellow persists (in one)." *Signalosa*: dorsal pigment intense blackish-brown; no distinct dorsal stripe; color on dorsum extends about one-fourth distance down sides; dorso-lateral scales each with discrete groups of melanophores near posterior margins, giving dorsum a lined appearance that is somewhat obscured by over-all color; "humeral spot jet black, bordered behind, below, and before by light areas, slightly confluent with dorsal pigment above; humeral spot smaller than orbit; humeral bar absent; lower abdominal area suffused with yellow, culminating in canary yellow on breast;" lateral region with small punctulations, giving appearance of dusky band in some specimens; "posterior ventral region silvery, with yellowish cast."

Fins.—*D. cepedianum*: dorsal and anal fins with black pigment on rays, scattered melanophores on interradi al membranes; pectoral fins with black on anterior rays and near fin tips, semi-clear between; pelvic fins totally black in some specimens, grading to black near tips and clear at base; caudal fin with blackened rays, caudal band rarely evident; no yellow colors noted in life, or in preserved material. Hybrids: black pigmentation of dorsal, pectorals and caudal generally as in *Signalosa*; yellow pigments of fins "as in *Signalosa*, possibly more intense." *Signalosa*: "dorsal fin with over-all gray appearance, rays darker; pectoral fins with dark melanophores present on anterior rays, most intense on posterior edge of first major ray, becoming diffuse near end of fin; proximal portion of fin slightly yellow, becoming more intense near base; pelvic fins with little or no dark pigment, canary yellow near base, grading to clear at tips; anal fin largely clear, with intense canary yellow along base; caudal fin with dark pigment on dorsal lobe to most dorsal rays, and on ventral lobe to second or third most ventral rays, extending about two-thirds of length of fin, becoming less intense, then reappearing as a black line on extreme posterior edge; extreme bases of rays in ventral lobe of caudal yellow, extending onto and throughout the length of the two or three ventral rays, and onto semi-transparent band running dorso-ventrally on the fin."

DISTRIBUTION OF *S. petenensis*

The range of the threadfin shad (including *Dorosoma petenense* and *D. mexicana*) was given by Jordan & Evermann (1896: 416-417) as the "east coast of Mexico" to Lake Peten (Guatemala). Evermann & Kendall (1898: 127) erected the name *Signalosa* and described *S. atchafalayae*, thus defining the known range as the "coast of Louisiana" to Lake Peten (Jordan, Evermann & Clark, 1930:46-47). In 1925, Weed (1925) recorded *Signalosa* from Florida (as *S. atchafalayae vanhyningi* Weed); Miller (1950:390) recorded the range as "Atlantic [Coast] (from Florida to northern Guatemala and British Honduras)."

In 1948, fishery workers for the Tennessee Valley Authority found threadfin shad in the large Tennessee River impoundments (Anonymous, 1954). Within a few years the species had spread to all of the mainstream reservoirs on the Tennessee River. Apparently, small numbers of *S. petenensis* had been present in the lower Tennessee River and had rapidly increased in numbers when more stable conditions were created by the reservoirs. This northern acclimatization of the threadfin shad was recently

recorded by Moore (1957:59-60) in his statement of its range: "Gulf Coast from Florida to Texas, northward in Mississippi Valley to Tennessee and southern Arkansas and Oklahoma and southward to British Honduras."

With the increase in abundance in the Tennessee River Basin, the value of this small, prolific "forage-fish" soon was recognized by workers from other areas. Between 1948 and 1953 the species was introduced into other impounded waters in Tennessee with general success (Anonymous, 1954; Parsons & Kimsey, 1954); according to Parsons & Kimsey, however, the threadfin shad had not been recorded in the Cumberland River System as of 1954. Parsons (1957) recorded the species from the Cumberland System (Center Hill Reservoir), but failed to state whether the fish was native or had been introduced. He did, however, record the stocking and establishment of *S. petenensis* in Dale Hollow Reservoir in 1955.

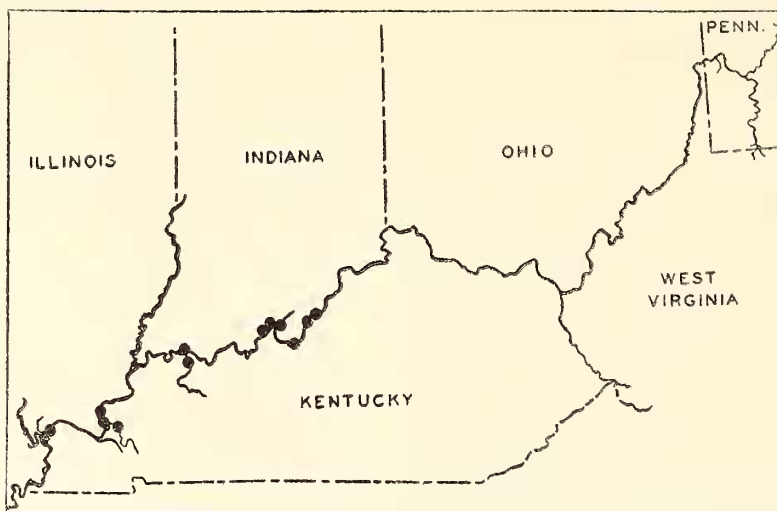
After a practical method of transporting the threadfin shad had been found (Parsons & Kimsey, 1954), it was stocked widely in the United States. Mr. Charles J. Chance, Tennessee Valley Authority, has informed us (personal communication, Dec., 1959) that "Threadfin shad . . . have gone either directly or indirectly from the [Tennessee River] Valley to the following places: Virginia, Georgia, Pennsylvania . . . California, Nevada, Arizona, Kansas . . . and New Mexico. We understand that they were transported from California to the Hawaiian Islands where they have potential use in chumming tuna." The species had been introduced into California in November, 1953 (Kimsey, 1958). The stock was held in San Diego County until 1954 and 1955, when their progeny were released in Lake Havasu, California. By September 1955, threadfin shad were found near Brawley, in the Salton Sea and near the Imperial Wildlife Refuge in California, and near Yuma, Arizona (Kimsey, *loc. cit.*). According to Haskell (1959:298), the species was subsequently stocked "in other impoundments up and down the [Colorado] river by both California and Arizona, and the species was also introduced into the deep-water lakes of central Arizona." Haskell also noted that the establishment of the species in western waters had been easily accomplished because of "biological explosions" that occurred shortly after stocking.

Threadfin shad are now also established in Virginia (Parsons, 1957) and in West Virginia (Schwartz, 1958), the latter occurring in the Ohio River Basin as a result of the downstream movement of threadfin shad from Virginia plantings in the upper Kanawha River System.

Threadfin shad introduced into Kansas failed to survive the winter (Parsons & Kimsey, 1954) and the species probably met a similar fate in Pennsylvania (Charles J. Chance, personal communication). An attempted introduction into hatchery ponds in southern Indiana in 1958 was unsuccessful (W. B. Barnes, personal communication). The results of the introductions into Nevada, Georgia and Hawaii are unknown to us.

The assumption that the threadfin shad is a new invader of the waters of the Ohio River is, of course, based on negative evidence. The species was not recorded from the lower Ohio in such exhaustive works as Forbes & Richardson (1904, 1920) in Illinois, Gerking (1945) in Indiana, and Trautman (1957) in Ohio. Moreover, the extensive surveys of the Upper Mississippi River Conservation Commission (1945-1959), reported in detail in Barnickol & Starrett (1951) and others, failed to record the threadfin shad in the vicinity of the mouth of the Ohio River, or in the Mississippi River above the mouth of the Ohio.

The information given above on the introduction and occurrence of the threadfin shad in Pennsylvania and West Virginia (the latter records are known to be in the Ohio Basin) brings up the possibility of downstream movement of the species from upstream stockings. However, the survey in which our specimens were obtained included collections from the entire length of the Ohio River, and no threadfin shad were collected farther upstream than the vicinity of Louisville, Kentucky. From the "lower river" (downstream from the vicinity of Louisville), *S. petenensis* was taken in 25 of the 62 collections that were made with gear that might be expected to capture this species. Our collections of threadfin shad in the Ohio River range from approximately 10 miles upstream from U. S. Government Lock No. 41, at Louisville, downstream to near the mouth of the river near Mound City, Illinois (Text-fig. 2). The localities plotted in Text-fig. 2, with the exception of those localities and/or dates for the specimens listed previously in this paper, are: *Illinois*. Massac Co., Massac Creek, near its confluence with the Ohio River, Sept. 9, 1957; Pulaski Co., Cache River, 1.0 miles upstream from Ohio River, near Mound City, Sept. 10, 1957; and Pope Co., Big Bay Creek, Sept. 10, 1957, and Grand Pierre Creek, near their confluences with the Ohio River, Sept. 11, 1957. *Indiana*. Harrison Co., Indian Creek, near its confluence with the Ohio River, Aug. 15, 1957; and Crawford Co., Little Blue River, near Alton, Aug. 16, 1957. *Kentucky*. Ballard Co., Ohio River, Lock No. 53, near Grand Chain, Massac Co., Illinois, Oct. 29,



TEXT-FIG. 2. Map of the Ohio River showing the locations referred to in this report where specimens of *Signalosa petenensis* were collected.

1957, and Ohio River, near Mound City, Pulaski Co., Illinois, Aug. 25, 27, 1959; Livingston Co., Ohio River, at Lock No. 51, near Golconda, Pope Co., Illinois, July 18, 1957; Daviess Co., Ohio River, Lock No. 47, near Newburgh, Warrick Co., Indiana, Dec. 2-3, 1957; Meade Co., Ohio River, Lock No. 44, near Leavenworth, Crawford Co., Indiana, Nov. 26, 1957; Hardin Co., Ohio River, at West Point, July 8, 1959; Jefferson Co., Ohio River, Lock No. 41, at Louisville, Sept. 17, Oct. 22, Nov. 21, Dec. 17, 1957, Jan. 30, 1958, Sept. 9, 1959, Ohio River, at Sand Island, 0.5 mile downstream from Lock No. 41, Nov. 5, 1957, Ohio River, at the north end of Dam No. 41, July 9, 1959, and Ohio River, Sixmile Island, upstream from Louisville, Nov. 21, 1959.

The numbers of *S. petenensis* in our collections ranged from single specimens to a maximum of over 10,000 young of the year that were taken by brief seining at the station at Hardin County, Kentucky. The greatest number of adult specimens taken in one sample was 2,770; these were obtained by rotenone from Lock No. 53 on the Ohio River near Grand Chain, Illinois.

DISCUSSION

The occurrence of the hybrid fishes described here is of special interest in light of the apparent recent movement of one of the parental species, *S. petenensis*, into the Ohio River Basin. This invasion is of interest from the point of view of determining the factors that permitted the increase in range of the species. The movement of

S. petenensis into the Ohio River was undoubtedly augmented by the presence of navigation dams and their probable (but relatively undocumented) effect on the stability of water levels and temperature. That the threadfin shad is sensitive to low temperatures is attested by the records of temperature-induced mortality in Texas (Hubbs, 1951:297) and in Alabama (Anonymous, 1954), where sudden drops in temperature to about 50 degrees F. or less occurred. Parsons & Kimsey (1954), however, noted "heavy mortality" when threadfin shad, which were being transported, were subjected to temperatures lower than 45 degrees F. Apparently, the threadfin shad can withstand water temperatures lower than 50 degrees if they are lowered slowly, or, as an alternative, the stocking of the threadfin shad in Tennessee Valley may have made possible the selection of a cold-resistant form, which then continued to penetrate into the cooler waters of the Ohio River. Acclimatization of this sort was described by Krumholz (1944) for *Gambusia affinis* (Baird & Girard) after stocks of this species had been transferred from near Carbondale, Illinois, to northern Illinois and thence to Michigan and other northern states.

The lock and dam emplacements on the Ohio River obviously have not prevented the movement of *S. petenensis* upstream. The dam at Louisville, however, is at present the highest on the Ohio River, being approximately 37 feet at "normal pool," and could be a major deterrent.

The causes of hybridization between *Signa-*

losa and *Dorosoma cepedianum* are unknown; however, some conclusions may be drawn in light of recent remarks on causes of hybridization in other freshwater fishes by Hubbs (1955). The gizzard shad is a very abundant fish in the Ohio River, exceeding the relative abundance of all fishes in weight and being exceeded in number only by certain minnows. Conversely, the threadfin shad is relatively rare, comprising considerably less than 5 percent of all fishes taken in 19 of the 25 collections in which it occurred. In addition, the threadfin shad is presumed to be a new, or relatively recent, invader following the man-made alterations in the Ohio River. All three of these factors, viz., (1) the rarity of species, (2) the introduction or recent invasion of one species and (3) the alteration of the environment by man, were cited by Hubbs (1955) as factors bringing about the breakdown of "species lines" in fishes. It seems probable that hybridization between these two shads occurred as a result of the less abundant threadfin shad joining spawning aggregations of *D. cepedianum*.

SUMMARY

This paper concerns the first known natural hybrids between the gizzard shad, *Dorosoma cepedianum* (LeSueur), and the threadfin shad, *Signalosa petenensis* (Günther). Six specimens of this hybrid combination, all from the Ohio River, are compared with 25 specimens of each parental species from the same general area. The hybrids were intermediate in most proportional and meristic characters examined; however, in characters involving plumpness of body and development of fins, the hybrids were extreme. The extreme development of these characters is attributed to complementary action of genes. Basic color patterns of the hybrids resembled *Signalosa* more closely than *Dorosoma*, but mingling of the two patterns was obvious.

Signalosa is a recent invader of the Ohio River Basin, and a review of the current distribution of the species is included. The recent invasion of the Ohio River Basin by one species, the modifications of that basin by man's activities, and the relative rarity of *Signalosa* are probably all contributory to the breakdown of the isolating mechanisms between these two clupeids, and the subsequent miscegenation.

LITERATURE CITED

ANONYMOUS

1954. The shad called threadfin. Prog. Rept., Jan., 1954, Tennessee Valley Authority, Div. For. Rel., 1 p., mimeographed.

BAILEY, REEVE M., HOWARD E. WINN & C. LAVETT SMITH

1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Nat. Sci., Philadelphia, 106: 109-164.

BARNICKOL, PAUL G., & WILLIAM C. STARRETT

1951. Commercial and sport fishes of the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. Bull. Illinois Nat. Hist. Surv., 25 (5): 267-350.

BERG, LEO S.

1940. Classification of fishes, both recent and fossil. Trav. Inst. Zool. Acad. Sci. USSR, 5 (2): 87-517

DOBZHANSKY, THEODOSIUS

1952. The nature and origin of heterosis. Pp. 218-223 of "Heterosis." John W. Gowan, Editor. Iowa State College Press, Ames, Iowa.

EVERMANN, BARTON W., & WILLIAM C. KENDALL

1898. Descriptions of new or little known genera and species of fishes from the United States. Bull. U.S. Fish. Comm., 17 (1897): 125-133.

FORBES, STEPHEN A., & ROBERT E. RICHARDSON

1904. "The Fishes of Illinois." Illinois State Nat. Hist. Surv., cxxxvi + 357 pp.
1920. *Ibid.* (Second Edition).

GERKING, SHELBY D.

1945. Distribution of the fishes of Indiana. Invest. Indiana Lakes and Streams, 3 (1): 1-137.

HASKEL, WILLIAM L.

1959. Diet of the Mississippi threadfin shad, *Dorosoma petenense atchafalaya*, in Arizona. Copeia, 1959 (4): 298-302.

HUBBS, CARL L.

1955. Hybridization between fish species in nature. Syst. Zool., 4: 1-20.

HUBBS, CARL L., & E. ROSS ALLEN

1945. Fishes of Silver Springs, Florida. Proc. Florida Acad. Sci., 6 (1943): 110-130.

HUBBS, CARL L., & LAURA C. HUBBS

1931. Increased growth in hybrid sunfishes. Pap. Michigan Acad. Sci., Art. and Lett., 13 (1930): 291-301.
1932. Experimental verification of natural hybridization between distinct genera of sunfishes. *ibid.* 15 (1931): 427-437.
1933. The increased growth, predominant maleness, and apparent infertility of hybrid sunfishes. *ibid.* 17 (1932): 613-641.

- HUBBS, CARL L., LAURA C. HUBBS & RAYMOND E. JOHNSON
1943. Hybridization in nature between species of catostomid fishes. Contr. Lab. Vert. Biol. Michigan, No. 22, 72 pp.
- HUBBS, CARL L., & KATSUZO KURONUMA
1942. An analysis of hybridization in nature between two species of Japanese flounders. Pap. Michigan Acad. Sci., Art. and Lett., 27 (1941): 267-306.
- HUBBS, CARL L., & KARL F. LAGLER
1958. Fishes of the Great Lakes Region. Bull. Cranbrook Inst. Sci., No. 26 (Revised Edition), xiii-213 pp.
- HUBBS, CARL L., & ROBERT R. MILLER
1943. Mass hybridization between two genera of cyprinid fishes in the Mohave Desert, California. Pap. Michigan Acad. Sci., Art. and Lett., 28 (1942): 343-385.
- HUBBS, CLARK
1951. Minimum temperature tolerances for fishes of the genera *Signalosa* and *Herichthys* in Texas. Copeia, 1951 (4): 297.
1956. Relative variability of hybrids between the minnows *Notropis lepidus* and *N. proserpinus*. Texas Jour. Sci., 8 (4): 463-469.
- HUBBS, CLARK & KIRK STRAWN
1956. Interfertility between two sympatric fishes, *Notropis lutrensis* and *Notropis venustus*. Evolution, 10 (4): 341-344.
1957a. Survival of F₁ hybrids between fishes of the subfamily Etheostominae. Jour. Exp. Biol., 134 (1): 33-62.
1957b. Relative variability of hybrids between the darters *Etheostoma spectabile* and *Percina caprodes*. Evolution, 11 (1): 1-10.
- JORDAN, DAVID S., & BARTON W. EVERMANN
1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus., No. 47 (Part 1), 1,240 pp.
- JORDAN, DAVID S., BARTON W. EVERMANN & HOWARD W. CLARK
1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. App. X, Rept. U.S. Comm. Fish. for 1928. 670 pp.
- KIMSEY, J. BRUCE
1958. Introduction of the redeye black bass and the threadfin shad into California. California Fish and Game, 40 (2): 203-204.
- KRUMHOLZ, LOUIS A.
1944. Northward acclimatization of the western mosquitofish *Gambusia affinis affinis*. Copeia, 1944 (2): 82-85.
- LINDER, ALLAN D.
1958. Behavior and hybridization of two species of *Etheostoma* (Percidae). Trans. Kansas Acad. Sci., 61 (2): 195-212.
- MARTIN, W. R.
1949. The mechanics of environmental control of body form in fishes. Univ. Toronto Stud., Biol. Ser., 58: 1-91.
- MILLER, ROBERT R.
1950. A review of the American clupeid fishes of the genus *Dorosoma*. Proc. U.S. Nat. Mus., 100 (3267): 387-410.
1960. Systematics and biology of the gizzard shad (*Dorosoma cepedianum*) and related fishes. Fish. Bull. 173, Fish. Bull. Fish Wildl. Serv., 60:371-392.
- MOORE, GEORGE A.
1957. Fishes. Pp. 31-210 of "Vertebrates of the United States," by W. F. Blair, A. P. Blair, P. Brodtkorb, F. R. Cagle & G. A. Moore, McGraw-Hill Book Co., Inc., New York.
- PARSONS, JOHN W.
1957. The trout fishery of the tailwater below Dale Hollow Reservoir. Trans. Amer. Fish. Soc., 85 (1955): 75-92.
- PARSONS, JOHN W., & J. BRUCE KIMSEY
1954. A report on the Mississippi threadfin shad. Prog. Fish. Cult., 16 (4): 179-181.
- SCHWARTZ, FRANK J.
1958. Threadfin shad—a new forage fish for West Virginia. West Virginia Cons., June (1958), 2 pp.
- TRAUTMAN, MILTON B.
1957. "The Fishes of Ohio." Ohio State Univ. Press, Columbus. 683 pp.
- UPPER MISSISSIPPI RIVER CONSERVATION COMMISSION
1945-1959. Proceedings of the Annual Meetings. Mimeographed.
- WEED, ALFRED C.
1925. A review of the fishes of the genus *Signalosa*. Field Mus. Nat. Hist. Publ. 233, Zool Ser., 12 (11): 137-146.

EXPLANATION OF THE PLATE

PLATE I

Photographs of a representative specimen of *Dorosoma cepedianum* (A), and three of the hybrids referred to in the text.

PLATE II

Photographs of three of the hybrids referred to in the text, and a representative specimen of *Signalosa petenensis* (D).